GEOGRAPHIC HOMOGENITY AMONG INSECT COMMUNITIES IN NEOTROPICAL PARAMOS: A HYPOTHESIS TEST

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Resumen
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Se comparó las comunidades de insectos de varios páramos neotropicales con base en la literatura y en un muestreo hecho en el Cerro Chirripó, Costa Rica (9° 30'N; 83 30'W, altitud 3450 m) Un total de 8000 barridas de red produjo 144 morfoespecies en 16 órdenes. Diptera es el orden con más morfoespecies (70) seguido de Hymenoptera (23), Lepidoptera (18) y Coleoptera (15). Los grupos de insectos de microhábitats húmedos fueron los más diversos. Los adultos nectarívoros, y los que en su etapa inmadura son saprófagos, herbívoros y parásitos fueron los más abundantes. La composición taxonómica no difiere estadísticamente entre los páramos neotropicales considerados.

Palabras clave: Ecología, Insectos, Páramos.

Abstract
Insect communities of several neotropical paramos were compared using data from the literature and a sampling conducted at Cerro Chirripó, Costa Rica (9° 30'N; 83 30'W, altitude 3450 m). A total of 8000 net sweeps yielded 144 morphospecies within 16 orders. Diptera was the order with most morphospecies (70) followed by Hymenoptera (23), Lepidoptera (18) and Coleoptera (15). Groupe inhabiting humid microhabitats were more diverse. Adult nectarivores, and inmature saprophages, herbivores and parasites were most abundant. Statistical analyses were unable to reject the hypothesis that the taxonomic composition is similar among Neotropical paramos.

Introduction

Qualitative evidence suggests that past and present communities from climatically similar places have similar guild compositions (HAWKINS AND MACMAHON, 1989; SIMBERLOFF & DAYAN, 1991; DAMUTH, 1992). Nevertheless, the taxonomic groups in the guilds may not be the same (DESCIMON, 1986; DAMUTH, 1992). Another similarity, not mentioned in the literature known to us, is that the proportion of species of each macrotaxon may also be similar among equivalent communities. In the Neotropical highlands, research still concentrates on taxonomy and systematics (particularly of plants) and ecological work is scanty. In their valuable review of the New World paramos, STURM AND RANGEL (1985) argued for more zoological studies, especially of thropic relations in the paramo ecosystem.

This study, which considers the entomofauna by taxon, microhabitat and guild, was designed to test the hypothesis that their taxonomic composition is similar among Neotropical paramos.

Field site

The study site was the area around the main Cerro Chirripó Grande visitors' cabin (9° 30'N; 83 30'W), located in the Talamanca range, Costa Rica (map in KAPPELLE 1991). It has a long history of fire activity (some anthropogenic); the most recent fire burned the paramo in 1976 and slightly modified the proportions of taxa in the plant community (WEBER 1959, HORN 1989-1991).

In the Andean paramos, precipitation ranges from ca. 100 to 2850 mm, temperature can reach the freezing point, and the dry and rainy season peaks occur around February and July, respectively (SCHNETTER ET AL. 1976, STÜRM AND RANGEL 1985). In the Chirripó, annual means are near 2500 mm and 7.6 C, and the rainy season lasts from May to November (HORN 1990, 1991; KAPPELLE, 1991).

At the collection site (300 m around the ranger's station), vegetation is composed mainly of *Chusquea subtesellata, Pernettia coriacea, Valeriana pulchella, Geranium repens, Carex sp., Valeriana prionophylla, Hypericum consanguineum, Castilleja talamancensis* and *Pernettia prostata*. According to STÜRM & RANGEL (1985), some of these genera are "paramo indicators" in South America, although they can be considered pioneer species of high elevation favoured by fire (see HORN, 1991).

Methods

Round sweeping nets 40 cm in diameter were used for collection. The first collection (about 2000 sweeps) was done during the first week of Ausgust, 1987, a lower precipitation period of the rainy season. The second collection (about 6000 sweeps) was at the end of the rainy season (third week of Dec., 1988).

STÜRM & RANGEL (1985) have shown the importance of collecting with a variety of techniques, so we obtained additional samples with three Malaise traps (1.93X1.60X1.15 m), some hand picking under pebbles, and shovel loads of the upper 2 cm layer of ground and covering debries, according to Bernal (in STÜRM & RANGEL 1985). These were mainly *C. subtesellata* leaves; six samples of aproximately 600 gr (each visit) were taken. The fauna was extracted with Berlese funnels (sun-heated for two consecutive days) in the first visit, and by hand in the second (overcast days prevented the use of sun heat).

Feeding guilds and habitat were determined from the literature (BORROR ET AL. 1976, ESSIG 1954) and field observations. Identifications are based on BORROR ET AL. (1976) and vouchers of all orders are deposited in the collections of the Universidad de Costa Rica and Museo Nacional de Costa Rica. All data were analysed with contingency chi-square tests.

Results and discussion

The study was designed to anlyze the entomofauna by taxon, habitat and guild, although some data on abundance are also included.

THE CHIRRIPO PARAMO

Taxonomic composition

The insects collected in the Chirripó paramo fit Mani's (1962) observation of melanization and small size: most are dark brown and measure less than 3 mm in body length. In total, forty insect families were found, not far from the figure of 57 reported by BERNAL (in STÜRM & RANGEL 1985) for South America. Net sweeping produced individuals of all mayor orders, while the Malaise traps were low in Coleoptera (second sampling, Table 1, $p < 0.01$). Ground sampling practically lacked representation of Diptera, Hymenoptera and Lepidoptera. Generally, the order Diptera had most individuals (Table 1).

A total of 144 morphospecies of 16 orders were collected (Appendix 1, based on the first sampling). Diptera is also the order with most morphospecies (70 distributed in 20 families) followed by Hymenoptera (23 in eight families), adult Lepidoptera (18 in three) and Coleoptera (15 in nine, Appendix 1). The high morphospecies richness of Diptera (Figure 1) has been observed in Costa Rican, South American and Asian highlands (Stürm & Rangel, 1985; Stürm 1989 and references cited in Figure 1).

Microhabitats and guilds

Dwellers of humid microhabitats are diverse, while there are relatively few hygrophilic and geophilous morphospecies; the soil is mostly occupied by preimaginal stages, particularly coleopterans (Tables 2 and 3, chi-square <.01). Adaptation to moist and hipogeous habitats occurs in relatively less taxa than in the more extreme Himalayan conditions (see Mani 1962, 1968).

Table 1. Entomofauna of the paramo at Cerro Chirripó: number of specimens according to the collecting method.

	Diptera	Hymenoptera	Coleoptera	Lepidoptera	Others	
Sweeping	284	39	14	12	355	net
Malaise traps	210	25	1	25	13	
Berlese funnels	1	0	10	1	33	
Total	495	64	25	38	401	

Table 2. Habitats of adult insects from the Chirripó paramo. All figures are number of morphospecies.

Habitat	Diptera	Hymenoptera	Lepidoptera	Coleoptera	Other Orders
Geophilous	—	3	—	7	6
Hygrophilous	—	—	—	—	1
Moist place	27	—	—	1	1
Other	40	20	18	5	10
Undetermined	3	—	—	2	—
Total	70	23	18	15	18

Table 3. Habitats of inmature insects from the Chirripó paramo. All figures are number of morphospecies.

Habitat	Diptera	Hymenoptera	Lepidoptera	Coleoptera	Other Orders
Geophilous	34	3	—	10	6
Hygrophilous	10	—	—	1	1
Moist places	—	—	—	1	1
Other	23	20	18	—	10
Undetermined	3	—	—	3	—
Total	70	23	18	15	18

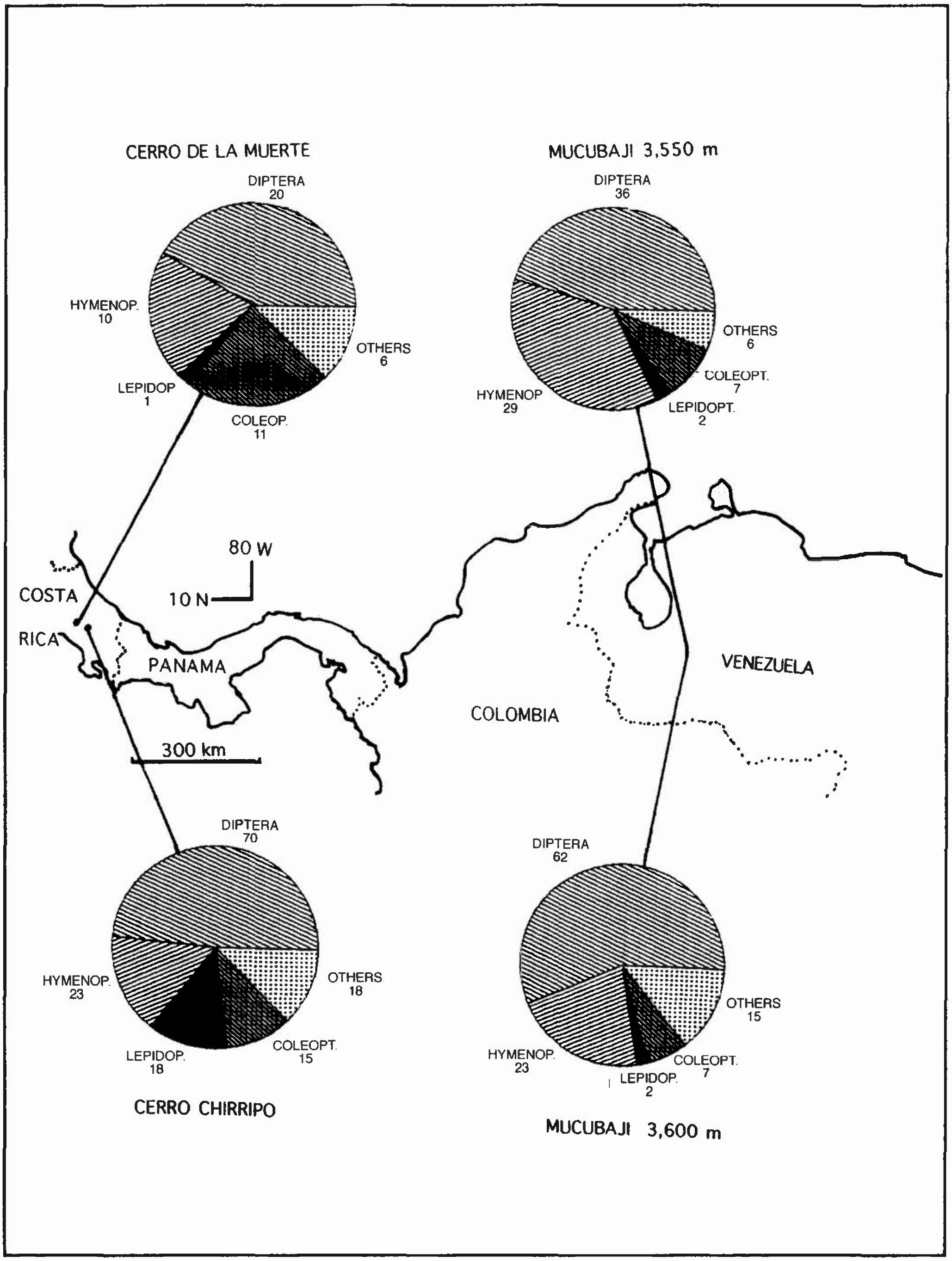

Figura. 1. Number of species of each insect group in four Neotropical paramos. Chirripó is 3,450 m above sea level and Cerro de la Muerte is lower (3.380 m). Sources: Janzen, 1976 and this paper.

Within trophic guilds, numbers of morphospecies are highest for adult nectarivores (Table 4, p<.01), and for inmature saprophages, herbivores and parasites (Table 5, p <.01). In comparison with a nearby lowland tropical site (Guanacaste, data in Janzen 1968), the Chirripó Paramo has more herbivorous and fewer carnivorous, parasitic and scavenging species, opposite to the highland-lowland relationship predicted by Mani for the temperate region (1962).

Several authors have found carnivorous and scavenging guilds to be particularly abundant in some highlands, where net plant productivity is low and herbivores relatively scarce but prey and detritus arrive frequently from lover habitats (Mani 1962, Edwards 1987). This suggests two hypotheses for the abundance of herbivores in the Chirripó paramo: (1) higher plant productivity and herbivorous activity, or (2) finer niche compartmentalization.

The first hypothesis does not fit the situation in the Southamerican paramos, the only for which date are available. For example, less than 10% of the *Espeletia* biomass is consumed by herbivores (Stürm and Rangel 1985). The second hypothesis (many rare species with a relatively low impact as herbivores) is consistent with the frequent fires reported for the Chirripó paramo (Horn 1989), because one effect of fire in the Southamerican paramos is a reduction of numerical dominance by any individual species (Stürm and Rangel 1985). Plant growth and probaly also productivity are low in the paramo as shown by fire recovery studies (Horn 1991).

Table 4. Feeding guilds of adult insects from the Chirripó paramo. No parasitic species were found. All figures are number of morphospecies. ^ nectarivorous includes polinophagous.

Guild	Diptera	Hymenoptera	Lepidoptera	Coleoptera	Other Orders
Predacious	2	—	—	6	1
Phytophagous	—	—	—	8	9
Nectarivorous^	61	23	18	—	1
Saprophagous	1	—	—	—	1
Omnivorous	—	—	—	—	5
Does not feed	—	—	—	—	1
Undetermined	6	—	—	1	—
Total	70	23	18	15	18

Table 5. Feeding guilds of inmature insects from the Chirripó paramo. All figures are number of morphospecies. ^ Nectarivorous includes polinophagous.

Guild	Diptera	Hymenoptera	Lepidoptera	Coleoptera	Other Orders
Predacious	8	—	—	6	1
Phytophagous	6	—	18	5	10
Nectarivorous^	—	2	—	—	1
Parasitic	9	21	—	—	—
Saprophagous	42	—	—	2	1
Omnívorous	—	—	—	—	5
Fungivorous	—	—	—	1	—
Undetermined	5	—	—	1	—
Total	70	23	18	15	18

Community composition: Test of hypothesis

The species richness of orders (Figure 1) is similar among the paramos (p >.05) but differs from those of both higher and lower ecosystems (see Mani 1962, Janzen 1968, Janzen et al. 1976). Compared with lowlands, paramos are poor in species of Hymenoptera and Lepidoptera, whose nectarivorous guild may be occupied by the more abundant Diptera (Tables 1 and 2). Coleoptera are species-poor in these paramos, even when compared with the Himalayas (Mani 1962), but the situation may be different in oher paramos which were not considered in this study.

The taxonomic homogenity of the paramos studied here may be explained by several hypotheses, including ecological convergence and common origin. Taxonomic subgroups have a close genetical basis which may lead to repeated occupation of certain guilds (see Schoenly et al. 1991). Guilds in turn have associated biomass and diversity values set by energetical limitations (Odum, 1969; Simberloff & Wilson, 1970; Schoenly et al., 1991). This would imply, for example, that Diptera could occupy the same guild in several paramos independently, and then its biomass and number of species would converge because of the energy budget typical of the paramo.

It was recently found that a high proportion of paramo plants require animal pollination (Ricardi *et al.* 1987) and we collected many dipterans that feed on the flowers. This suggests a possible relation between pollination and the abundance and diversity of Diptera in this area. In contrast, Janzen (1991: pers. com.) believes that the causes are abundance of detritus and the scarcity of parasitoids are more probable causes for the abundance of Diptera in highlands (see also Janzen et al. 1976). Saprophagous adult dipterans are abundant, perhaps in relation with slow rates of recomposition.

The second option, common origin, implies that currently isolated paramos have similar compositions because they have conserved the general community pattern that was present before isolation in recent geological times (see Simpson 1974). This hypothesis seems less probable because much of the Chirripó entomofauna did not vicariate from South American paramo lineages but evolved from lowland species (Halffter 1987). The characteristics of vicariant biogeographic analysis (Nelson & Rosen 1981) would make it particularly suited for any future test of these hypotheses.

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Apendix 1. Invertebrates from the Chirripó paramo (total = 144 morphospecies).

O. Diptera			(70)
	Agromyzidae		(1)
		Phytobia sp	
	Bibionidae		(2)
	Calliphoridae		(1)
	Cecidomyiidae		(1)
	Chironomidae		(10)
	Dolichopodidae		(1)
	Empididae		(1)
	Lauxaniidae		(1)
	Muscidae		(10)
	Mycetophilidae		(4)
	Phoridae		(2)
	Psychodidae		(1)
	Sarcophagidae		(2)
	Sciaridae		(1)
	Sciomyzidae		(1)
	Simuliidae		(1)
	Syrphidae		(6)
	Tachinidae		(9)
		Dejaria sp	
		Saundessia 2spp	
		Degeneria sp	
		Rhinophora sp	
	Tephiritidae		(3)
		Tephritis sp	
		Carphotricha sp	
	Tipulidae		(7)
	Undetermined		(5)
O. Hymenoptera			(23)
	Andrenidae		(1)
	Apidae		(1)
		Bombus sp	
	Braconidae		(4)
	Ceraphronidae		(1)
	Eulophidae		(3)
	Ichneumonidae		(11)
		Netelia sp	
	Pteromalidae		(1)
	Torymidae		(1)
O. Lepidoptera			(18)
	Geometridae		(3)
	Pterophoridae		(1)
	Sphingidae		(1)
		Aelopus titan	
	Undetermined		(13)
O. Coleoptera			(15)
	Anthribidae		(1)
	Carabidae		(3)
	Curculionidae		(3)
		Phyllotrox sp	
	Chrysomelidae		(1)
	Elateridae		(1)
	Lampyridae		(1)
		Photinus sp	
	Lycidae		(1)
	Melolonthidae		(2)
		Ancognatha sp	
		Golofa sp	
	Staphylinidae		(1)
	Undetermined		(1)
O. Homoptera			(5)
	Aphididae		(2)
	Cicadellidae		(2)
	Psyllidae		(1)
O. Orthoptera			(2)
	Acrydiidae		(1)
	Blattidae		(1)
O. Collembola			(2)
	Entomobrydae		(1)
	Poduridae		(1)
O. Psocoptera			(1)
	Psocidae		(1)
O. Hemiptera			(1)
	Lygaeidae		(1)
O. Thysanoptera			(1)
	Thripidae		(1)
O. Thysanura			(1)
	Campodeidae		(1)
O. Protura			(1)
O. Tricoptera			(1)
O. Dermaptera			(1)
O. Ephemeroptera			(1)
O. Neuroptera			(1)
	Hemerobiidae		(1)

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